I. Mackenzie Lamb*: The species of Stereocaulon with protosacculate cephalodia

I·マッケンジー・ラム: 原生嚢状頭状体をもつキゴケ属地衣

The writer (Lamb, 1951) drew attention to the fact that sacculate cephalodia in Stereocaulon may be of two distinct types, either solid or loosely hyphose internally. Cephalodia of the former solid-cored type were later designated as protosacculate (Lamb, 1961). Sacculate cephalodia, generally, are distinguished by their smoothly corticate, even to foveolate or scrobiculatecorrugated surface and especially by the structure of their cortex, which is well developed, usually clear and hyaline in section, and highly gelatinized, with the swollen walls of the hyphae entirely coalescent and indistinguishable, only the hyphal lumina being visible. The shape of these lumina varies in different species or to a certain extent within the same species. They may be narrow, thread-like, and closely radially parallel (palisadic); thread-like and randomly interwoven in various directions; broader and oblong, mainly radially parallel; or comparatively large, round and isodiametric (Lamb, 1951, fig. 2). Sometimes a combination of two or more different types is found in the same cortical layer, as figured by Lamb (1961, fig. 2a). The internal tissue of protosacculate cephalodia, in which the blue-green algae (almost invariably Nostocoid) are embedded, is solid and compact, without air-spaces, colorless and hyaline. In spite of their internal solidity, such cephalodia may become foveolate and more or less scrobiculate, although never so strongly as in some species with loose-cored cephalodia, e.g. St. ramulosum (Sw.) Räusch. Sometimes (notably in St. botryophorum Müll. Arg.) they may become subdivided into verrucose portions. With some practice they may be recognized as protosacculate by their external appearance, but in cases of doubt, and for the study of the cortical structure, it is necessary to cut sections.

Protosacculate versus loose-cored cephalodia have proved to afford a valuable and obviously natural taxonomic criterion delimiting a related assemblage of species in subgen. *Holostelidium* sect. *Sacculata* (Lamb, 1951). It is this

^{*} Farlow Herbarium, Harvard University, Cambridge, Mass., U.S.A.

assemblage which is now dealt with taxonomically in the present treatment. Cephalodia which are technically more or less solid-cored, but not to be regarded as of the truly protosacculate type, occur in some other, not closely related, species of the genus. Thus the New Zealand species St. caespitosum Redgr. and St. gregarium Redgr. (subgen. Holostelidium sect. Redingeria M. Lamb, 1951) have cephalodia which are almost solid-cored, but have also some loosely interwoven hyphae in their interior; they are not closely related to the truly protosacculate assemblage here considered. The cephalodia of the species of subgen. Holostelidium sect. Dactyloideum M. Lamb (1951), although likewise semi-solid internally, are distinct in external morphology, and do not indicate any close taxonomic relationship with the protosacculate group.

The following key includes all the *Stereocaulon* species known to date belonging to subgen. *Holostelidium*, sect. *Sacculata*, subsections *Aciculisporae* and *Ascaridisporae*, which have protosacculate (solid-cored) cephalodia.

Key

1. No phyllocladia present (completely replaced by soredia)

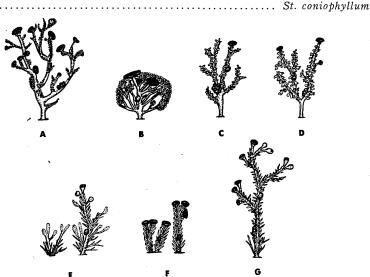


Fig. 1. Habitus of Stereocaulon species.

A, St. coniophyllum. B, St. Humbertii. C, St. botryophorum. D, St. foliolosum. E, St. claviceps. F, St. macrocephalum. G, St. pomiferum.

1a. Phyllocladia present; soredia absent or present
2. Phyllocladia verrucose, squamulose, or foliose, PD $-$ or $+$ pale yellow
no soredia
2a. Phyllocladia cylindrical, coralloid, usually PD $+$ red; soredia sometime
present
3. Pseudopodetia 1-2 cm long, densely branched and fastigiate-caespitose
phyllocladia concentrated at and towards apices of pseudopodetia, grain
like to thickly squamulose; apothecia large, 4-5 (-8) mm diam.; spore
3-6-septate, 45-60 μ long; cephalodial cortex with isodiametric, rounded o
subangulose lumina
3a. Pseudopodetia taller, up to 5 cm long, not densely fastigiate-caespitose
phyllocladia lateral on pseudopodetia, not concentrated at apices, thickly
squamulose, squamulose-subcoralloid, or flattened-foliose; apothecia smaller
1.5-3.5 mm diam.; spores longer and usually more septate; cephalodia
cortex with partly narrow, elongate lumina
4. Phyllocladia thickly squamulose to squamulose-subcoralloid or almost coral
loid; spores 3-11-septate, (20-) 30-110 μ long St. botryophorum
4a. Phyllocladia (at least mostly) flattened-foliose; spores 6-14-septate, (55-)
60-110 μ long
5. Phyllocladia all flattened-foliose St. foliolosum (var. foliolosum)
5a. Phyllocladia flattened-foliose below, becoming subcoralloid in upper parts
of pseudopodetia St. foliolosum (var. strictum)
6. Apices of pseudopodetia effusely sorediate St. clavicep.
6a. No soredia present
7. Plants small, pseudopodetia less than 3 cm long; apothecia not hypophysate
no distinct clayulae* developed; cephalodial cortex with isodiametric
round lumina 2.5-6.0 μ diam. intermixed with radially elongate, oblong
lumina 2-3 μ wide
7a. Plants larger, pseudopodetia (2.5-) 3-6 (-7) cm long; apothecia hypo
physate, arising in distinct swollen clavulae; cephalodial cortex mostly
with radial (palisadic) tubular lumina 1-2 μ wide, often also with an inner
or outer stratum of isodiametric, rounded lumina 2-4 μ diam. (rarely the
two types intermixed)

^{*} Term originated by Duvigneaud (1956, p. 107) to designate the apical pyriform swellings in which ascogonia are formed and apothecia develop in species of *Stereocaulon* with long, multiseptate spores.

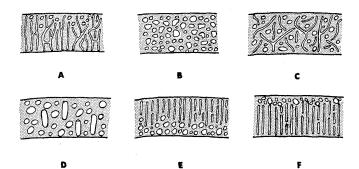


Fig. 2. Structure of cortex of protosacculate cephalodia of Stereocaulon species.

A, St. coniophyllum. B, St. Humbertii. C, St. botryophorum and St. foliolosum. D, St. macrocephalum. E and F, St. claviceps and St. pomiferum (two variant types).

Stereocaulon coniophyllum M. Lamb in Bot. Notiser, 114 (3): 266 (1961)

Pseudopodetia erect, firmly attached to rock, up to 5 cm long, robust, irregularly branched, glabrous, corticate on one side in apical parts and often spathulate-flattened at tips with the lower side sorediose. Phyllocladia not developed, replaced by effuse, confluent, granular-farinose soredia. Cephalodia lateral, sessile, subglobose or pulvinate, finally convolute-tuberculate or subdivided into verruciform portions, gray to brown; lumina of cortex mainly narrow and fistulose, palisadic or running in various directions and anastomosing, often also partly isodiametric and round. Algae of cephalodia Nostocoid (rarely Scytonema). Apothecia terminal, at first scutelliform, finally convex-immarginate, 1.5–4.0 mm diam., not arising in clavulae, no hypophysis developed. Excipulum 75–100 μ thick. Central cone compact, gelatinized, with enclosed aggregations of sordid granular substance. Hypothecium \pm colorless to faintly sordid isabelline. Hymenium 80–90 μ high. Spores 5–8, packed straight in ascus, (3–) 5–7-septate, straight or only slightly flexuose, 40–55 (–65) ×3.5–4.0 μ .

Mat. chim.: Atranorine and Lobaric acid (thallus-mantle and soredia PD + pale yellow).

This species has a widespread distribution, circumpolar-boreal with alpine outliers further south; it has been seen from Fennoscandia, Cetral Europe, Arctic Canada, Alaska, Japan and Nepal. In the protosacculate assemblage

it is a primitive species, as evidenced by the short, relatively pauciseptate spores. It may be a very ancient representative, persisting now only in relict stations, of a formerly widespread group of species now restricted to Africa and Asia.

Stereocaulon Humbertii Duvign. in Lejeunia, Mém. 14 (1955): 132 (1956) Pseudopodetia erect, firmly attached to rock, up to 2 cm long, densely fastigiately branched and congested, decorticate, rigid, glabrous. No soredia. Phyllocladia concentrated at and towards apices of pseudopodetia, crowded, granular to verrucose or thickly squamulose, small, 0.1–0.4 mm diam. Cephalodia lateral on pseudopodetia and apical among phyllocladia, pulvinate-subglobose, brown, ochraceous or glaucous, later dividing into convex portions or becoming fissured; their cortex gelatinized-pseudoparenchymatous (not palisadic) with ± isodiametric, rounded or subangulose cell-lumina; algae Nostocoid (Anabaena acc. to Duvigneaud, op. cit.). Apothecia (not often present) terminal, large, 4–5 (–8) mm diam., dark brown, scutelliform, finally subdivided into secondary discs; no hypophyses or clavulae developed. Excipulum 100–160 μ thick. Central cone compact, inspersed with masses of sordid granules. Hypothecium colorless, shallow. Hymenium 70–90 μ high. Spores 5–8, straight, (3–) 4–5 (–6)-septate, 45–60×(3.5–) 4.0–4.5 μ.

Mat. chim.: Atranorine and Lobaric acid (phyllocladia PD + pale yellow). The habitus is very similar to that of *St. botryosum* Ach. emend. Frey, with the pseudopodetia forming dense, compact clumps. It is apparently a rare species, seen only from a few localities in the high mountains of E. Central Africa (Kivu, Ruwenzori) at altitudes of 4000 to 5000 meters.

Stereocaulon botryophorum Müll. Arg. in Flora, 74: 371 (1891)

Pseudopodetia erect or subdecumbent, rigid, firmly attached, 2-5 cm long, irregularly sparingly branched, decorticate, glabrous. No soredia. Phyllocladia unevenly distributed on sides of pseudopodetia, thickly squamulose and subcrenulate or squamulose-subcoralloid to almost coralloid, 1.0-1.5 mm long, sometimes paler at tips. Cephalodia lateral, brown or brownish, sessile to shortly pedicellate, globose and up to 1.5 mm diam. or sometimes becoming compound-pulvinate, up to 6 mm diam. and botryosely divided into verruciform portions; cortex with elongated, narrow lumina running in various directions (rarely \pm palisadically parallel), mixed with isodiametric, rounded lumina; algae Nostocoid. Apothecia (not often present) terminal, 1.5-3.3 mm diam.,

at first plane-scutelliform, finally convex-immarginate. No clavulae developed. Excipulum 100-300 μ thick. Central cone compact, heavily inspersed with opaque, yellowish-gray substance. Hypothecium hyaline to sordid isabelline-cloudy in section. Hymenium variable in height, 75-135 μ . Spores straight or vermiform-sinuose, variable in length and septation, (20-) 70-112 μ long, 3.5-4.5 μ broad, sometimes only 3-5-septate, but when optimally developed 9-11-septate.

Mat. chim.: Atranorine and Lobaric acid (phyllocladia PD + pale yellow).

Apparently endemic to the Himalayan region (N. India, Nepal, Sikkim), where it occurs at altitudes of 3500 to 5000 meters. It is perhaps not specifically distinct from the following (St. foliolosum), being possibly only a modification with reduced or badly formed phyllocladia. The hymenium tends to degenerate early, so that fully developed spores are relatively seldom found.

Stereocaulon foliolosum Nyl., Synops. Lich. 1: 240 (1860)

Pseudopodetia $3.0-4.5\,\mathrm{cm}$ long, \pm erect but often of somewhat dorsiventral habitus, firmly attached to rock, irregularly sparingly branched, decorticate, glabrous or subglabrous. No soredia. Phyllocladia lateral on pseudopodetia, evenly distributed or more abundant on one side, flattened and leaf-like, $1.5-2.5\,\mathrm{mm}$ long, flabellately branched, paler on underside. Cephalodia lateral on pseudopodetia, $1-2\,\mathrm{mm}$ diam., brown, pulvinate or subglobose, sometimes imperfectly divided into verrucose portions; their cortex with elongated lumina running in various directions, not palisadic, often also with isodiametric, rounded lumina; algae Nostocoid. Apothecia terminal, without hypophyses or clavulae, up to $2\,\mathrm{mm}$ diam. or somewhat over, plane to slightly convex, with thin, finally excluded proper or pseudothalline margin. Excipulum 80–250 μ thick. Central cone compact, sordid and \pm opaque from inclusions of granular substance. Hypothecium colorless, clear or slightly cloudy in section. Hymenium 90–110 μ high. Spores 4–8, straight or rarely spirally contorted in ascus, straight to sinuose-vermiform, 6–14-septate, $60-95\times3-4\,\mu$.

Mat. chim.: Atranorine and Lobaric acid (phyllocladial squamules PD+pale yellow).

Known only from the Himalayan region (N. India, Nepal, Sikkim), at altitudes of 2000 to 4000 meters, and easily recognized by the bifacial, leaf-like phyllocladia.

Var. strictum (Bab.) M. Lamb in Canad. Journ. Bot. 29: 582 (1951)

Syn. St. ramulosum var. strictum Bab. in Journ. of Bot. 4: 250 (1852) pr. p., St. macrocephalum var. strictum (Bab.) Dodge in Ann. Cryptog. Exot. 2: 126 (1929); non St. strictum Th. Fr.

Differs from the typical state of the species (var. *foliolosum*) in having the phyllocladia in the upper parts of the pseudopodetia papillose to shortly coralloid, but showing transition downwards into the typical leaf-like form. The distribution is the same as that of var. *foliolosum*.

Stereocaulon claviceps Th. Fr., De Stereoc. et Pilophor. Comment., 21 (1857)

Pseudopodetia erect, (0.5-) 1.5-3.0 (-4.0) cm long, sparingly branched, decorticate, glabrous, firmly attached to rock. Soredia present on branchapices, whitish, farinose, effuse. Phyllocladia lateral on pseudopodetia, coralloid (subulate-cylindrical), 1-3 (-5) mm long, the larger lower ones branched. Cephalodia lateral or basal, 0.5-1.5 mm diam., subglobose, glaucous gray to pale brown, smooth or somewhat foveolate-indented; lumina of cortex partly isodiametric, rounded, and also (in outer part) narrower, tubular and palisadically arranged; algae Nostocoid. Apothecia terminal, 1.0-1.5 mm diam., arising in subglobose or pyriform clavulae which often persist as a swollen hypophysis below younger apothecia; at first thinly marginate with a smooth receptacle, finally convex-immarginate. Excipulum 140-200 μ thick. Central cone with small air-spaces, colorless to sordid isabelline, not nubilated, with or without opaque grayish inclusions. Hypothecium colorless to faintly isabelline in section. Hymenium 120-180 μ high. Spores 6-8, often spirally wound in ascus, vermiform, 10-21-septate, (80-) 100-180 \times 3.5-4.0 μ .

Mat. chim.: Atranorine and Stictic acid (phyllocladia PD + orange-red, at least at the tips; soredia PD + intense red).

This species seems to be endemic to the highlands of Mexico, where it is fairly common at altitudes of 2000 to 4000 meters. Material from other parts of the world formerly ascribed to it belongs to a different, non-sorediate species, *St. pomiferum*. Sterile pseudopodetia of *St. claviceps* are most conspicuously sorediate; as the apothecia mature the soredia become sparser and may be almost lacking in well-fruited plants. Specimens from higher altitudes may be very stunted and often sterile, with heavily sorediate pseudopodetia only 5–15 mm long, with the phyllocladia and cephalodia developed mainly at the base.

Stereocaulon macrocephalum Müll. Arg. in Flora, 74: 371 (1891)

Pseudopodetia erect, firmly attached at base, $1.5-2.8\,\mathrm{cm}$ long, simple or only once or twice branched, partially corticate, glabrous. No soredia. Phyllocladia abundant, clothing the pseudopodetia densely on all sides, coralloid (cornute-cylindrical), simple, $1.5-3.0\,\mathrm{mm}$ long. Cephalodia lateral on pseudopodetia, also sometimes at base, smoothly subglobose, up to 1 mm diam., brownish; lumina of cortex isodiametric and round or vertically oblong, not tubular or palisadic; algae Nostocoid. Apothecia terminal, $2-3\,\mathrm{mm}$ diam., not hypophysate and apparently not arising in distinct clavulae, at first with smooth proper margin, soon becoming convex and \pm immarginate. Excipulum massive, ca. $320\,\mu$ thick. Central cone with small spaces between the hyphae, appearing \pm opaque in section from included air and sordid granules. Hypothecium colorless or slightly grayish-cloudy. Hymenium $160-220\,\mu$ high. Spores 6-8, spirally wound in ascus, vermiform-sinuose, 18-26-septate, $108-150\,(-200)\,\mu$ long, $4-5\,\mu$ broad.

Mat. chim.: Atranorine and Stictic acid (phyllocladia PD + orange-red, at least at tips and where broken).

A rare Himalayan species, seen to date only from two localities in N. India and E. Nepal, on rocks at altitudes from 3500 to 4300 meters. It is possible that it may be conspecific with the following species (St. pomiferum), representing a stunted form, but it seems to differ, as far as can be judged from the two specimens seen, not only in smaller stature and different habitus but also in some other characters, such as the apparent lack of distinct clavulae and in the structure of the cephalodial cortex. St. piluliferum Th. Fr., to which St. macrocephalum is placed as a synonym by Zahlbruckner (1927) is a different species, with loose-cored cephalodia.

Stereocaulon pomiferum Duvign. in Lejeunia, Mém. 14 (1955): 119 (1956) Syn. St. claviceps var. pomiferum (Duvign.) M. Lamb in Ergebn. Forsch. Unternehmen Nepal Himalaya, 1(4): 352 (1966); St. mamillosum Duvign., op. cit. p. 111; St. mikenoense Duvign., op. cit. p. 126; St. claviceps var. yunnanense Hue in Nouv. Arch. Mus. Hist. Nat. Paris, ser. 3, 10: 251 (1898); St. macrocephalum var. yunnanense (Hue) Dodge in Ann. Cryptog. Exot. 2: 125 (1929); St. yunnanense (Hue) M. Lamb ex Asahina in Kihara, Fauna and Flora of Nepal Himalaya, 1 (1952-53): 50 (1955) (comb. inval.).

Pseudopodetia erect, firmly attached to rock, (2.5-) 3-6 (-7) cm long,

subsimple to sparingly irregularly branched, often branched subcorymbosely only towards the apex, decorticate or partially corticate, glabrous. No soredia. Phyllocladia abundant, clothing pseudopodetia densely in most parts, coralloid (acuminate-cylindrical), 1-3 (-5) mm long, the larger lower ones branched. Cephalodia lateral on pseudopodetia or sometimes basal, smoothly subglobose or finally moderately foveolate-indented or convolute-scrobiculate, sometimes fissured, 1-2 mm diam., glaucous gray to brown; lumina of cortex mostly narrowly tubular and palisadically arranged, often also in inner or outer part wider, isodiametric and round (rarely the two types intermixed); algae Nostocoid. Apothecia terminal, arising in subglobose to pyriform clavulae, at maturity 1-3 (-5) mm diam., with dark brown, finally convex disc and paler brown, smooth or conspicuously tesselate-granulate proper margin (receptacle), in younger stages with ± distinct swollen hypophysis. Excipulum 120-350 u thick. Central cone compact or with small air-spaces, gray and opaque in section. Hypothecium colorless to faintly isabelline-cloudy. Hymenium 120-200 (-270) u high. Spores 4-8, straight or irregularly contorted or spirally wound inside ascus, vermiform-sinuose, 10-22 (-30)-septate, (80-) 140-160 (-220) u long, 3.5-4.0 (-4.5) u broad.

Mat. chim.: Atranorine and Stictic acid, sometimes with Norstictic acid or Dendroidin as accessory constituents (phyllocladia, at least at tips and where broken, PD + orange-red). Exceptionally, as in one specimen seen from Bhutan, Stictic acid may be almost absent, only Atranorine and Dendroidin being present in appreciable quantity (phyllocladia PD + pale yellow). Hawaiian specimens seen contain Atranorine and Norstictic acid or Atranorine only, and may perhaps represent a distinct subspecies. Specimens containing Dendroidin have so far been seen only from Nepal and Bhutan, but not all of our material has been chromatographed for this substance.

The taxon distinguished by Hue as *St. claviceps* var. *yunnanense* represents the species in its optimally developed condition, with large apothecia, high hymenium, and very long spores with up to 30 septa; the apothecial margin (receptacle) is conspicuously tesselate-granulate (resembling the sculpture on a truffle). All these characters, however, show complete intergradation into those of the more common form of *St. pomiferum*, and it is impossible to separate plants of the "*yunnanense*" type taxonomically.

St. pomiferum has a widespread bicentric African-Asian distribution,

occurring in high mountains of E. Central Africa (Congo, Kenya, Uganda, altit. 2500-4200 m), the Himalayas (N. India, Nepal, Tibet, Bhutan, Sikkim, altit. 2500-4700 m), Cnina (Yünnan, alti. 3750-4000 m), Formosa, and Japan. There is also an outlying oceanic station in Hawaii (perhaps a distinct subspecies, cfr. supra), and one specimen has been seen from Peru; it was recorded by Nylander (1859) as "Stereocaulon claviceps", but the specimen in his herbarium, collected by Weddell, is typical St. pomiferum.

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Bibliography

著者は 1951 年にキゴケ属の嚢状頭状体 (sacculate cephalodia) に 2 型あることを指摘し、1961年には中心部が密な組織からできているものを原生嚢状頭状体 (protosacculate cephalodia) とした。本論文ではキゴケ属の Holostelidium 亜属、オオキゴケ節 (sect. Sacculata) のなかの Aciculisporae 亜節と Ascaridisporae 亜節に属し原生嚢状頭状体をもつ既知の種について検索表を掲げ解説を附した。

St. coniophyllum Lamb 本種はヨーロッパ,カナダの北極圏,アラスカ,日本およびネパールから知られていて,小数の隔壁をもつ短い胞子を作るので,原生嚢状頭状体をもつキゴケのなかで最も原始的な種である。 アトラノリンとロバール酸を含み,擬子柄は葉状枝を全くつけず全体に紛芽でおいわれている。

- St. Humbertii Duvign. 擬子柄は密な集団をつくる。 明らかに稀産種で、 東部中央アフリカの標高 4000-5000 m の高地の数地点から知られているだけである。アトラノリンとロバール酸を含み、粉芽をつけない。
- St. botryophorum Müll. Arg. 明らかにヒマラヤ特産で、同地方の標高 3500-5000 m 附近で産する。St. foliolosum に似ていて、その発育不全型とも考えられる。子囊層は早く退化することが多く、そのため成熟した胞子は稀である。 アトラノリンとロバール酸を含み、粉芽なし。
- **St. foliolosum** Nyl. ヒマラヤの 2000-4000 m の地域からだけ知られている。 扁平で腹背性のある 葉状枝をつけるのが特徴である。 アトラノリンとロバール酸を含み、粉芽なし。

分布その他は規準種と同じであるが、 擬子柄上部の葉状枝が 疣状または 短いサンゴ 状を呈するものを var. strictum (Bab.) Lamb とした。

- St. claviceps Th. Fr. 本種はメキシュの高地特産であるが同地域では普通にみられる。メキシュ以外の世界の各地から本種が報告されているが、それらは粉芽のない St. pomiferum とみなされるものである。子器をつけた擬子柄では粉芽は稀かあるいはなくなるが、無子器の擬子柄は顕著な粉芽をつける。 アトラノリンとスチクチン酸を含む。
- St. macrocephalum Müll. Arg. 北部インドおよび東ネパールの二地点からしか知られていないヒマラヤ特産の稀種である。St. pomiferum と同一種かもしれないが、地衣体が小型であるばかりでなく、子器の基部が棍棒状にふくらまないことや頭状体の皮層の構造などで区別される。アトラノリンとスチクチン酸を含む。
- St. pomiferum Duvign. 本種はアフリカとアジア両地域を中心に分布していて、いわゆる bicentric な分布を示す。 東部中央アフリカ (コンゴ、ケニヤ、ウガンダ、標高 $2500-4200\,\mathrm{m}$)、ヒマラヤ、雲南、台湾、日本に産し、さらにハワイとペルーからも知られている。 Hue がかつて記載した St. claviceps var. yunnanense は本種の特に発育のよいもので、大きい子器に 30 コもの隔壁のある胞子を作り、子器の果托の縁は著しく顆粒状を呈する。